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# GROWTH OF CORMORANT *Phalacrocorax carbo sinensis* CHICKS IN RELATION TO BROOD SIZE, AGE RANKING AND PARENTAL FISHING EFFORT

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ABSTRACT Growth parameters of Cormorant hatchlings are described in relation to brood size and age ranking of each chick within individual broods. Growth rates, expressed as body mass increment per day over the period of linear growth (5-30 days), ranged from 56.4-102.8 $g \cdot d^{-1}$ and were found to be independent of brood size and age ranking. Asymptotic fledging mass, logistic growth rate coefficient and age at point of inflection were estimated for 14 chicks measured up to ages of over 30 days. Estimated body mass and age at fledging (twice the age at point of inflection) were further used to estimate the energetic needs. The fastest growing chicks would require peak energy needs of 3022 $kJ \cdot d^{-1}$, the slowest growing of about 2050 $kJ \cdot d^{-1}$. Total energy needs throughout the nestling period ranged from 46 000 to 69 000 kJ, implying average daily requirements of 1300-1800 kJ. Individual energy needs were on average 40% higher and at the peak 47% higher in fast growing chicks than in slow growing ones. However, slower growth, as a means of energy saving, does not seem to be chosen for voluntarily by younger chicks in larger broods. Parental fishing effort (expressed as total amount of time spent on fishing trips) increased with brood size. Maintaining a foraging uptake of 3 $g \cdot min^{-1}$ of fresh fish, found in the field, and a flying distance of 20 km, a bottleneck is expected to occur at the period of maximum energy needs. In order to cover maximum needs a chick should be fed with an average of 632 g of fish per day. Such a food provisioning level can be achieved for three chicks at an uptake level of 3 $g \cdot min^{-1}$ of fresh fish. A range of other flying distances and uptake levels is also presented to indicate the margins.

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## INTRODUCTION

Avian parents aim at optimising their lifetime reproductive output. The reproductive output within a single breeding season is likely to be limited by the parents' ability to provide enough food to the growing chicks (Lack 1968). However, Drent & Daan (1980) mention a considerable number of cases where parents were found to raise smaller clutches than they experimentally proved to be able to. Reasons for this may be the risk of lessened adult survival because of the extra energy investment involved (Masman *et al.* 1989) or, in case no food limitation exists, a high risk of nest predation (Weathers & Sullivan 1989). Under circumstances of food limitation the raising of chicks generally involves high levels of energy expenditure during the breeding season (Drent & Daan 1980, Birt-Friesen *et al.* 1989).

The energetic demands of a brood of growing hatchlings, and thus the level of investment of parental energy, depend primarily on brood size. However, they may be affected as well by individual differences in growth rate (Ricklefs 1968, Drent & Daan 1980, Klaassen *et al.* 1992). A model predicting energetic requirements of growing hatchlings, developed by Ricklefs (1969, 1976, 1983, 1984), suggested that energy savings as a

consequence of a reduced growth rate would be slight and insignificant. Experimental evidence, however, has shown that slower growing chicks can save a considerable amount of energy, especially during the period of maximum growth and energetic requirements (Klaassen *et al.* 1992). Within any brood size, individual differences in growth rate may thus alter the level of investment of parental energy.

It has been shown that in Cormorants *Phalacrocorax carbo sinensis* from the colonies feeding off the Dutch freshwater lake IJsselmeer reproductive output is directly connected to the conditions of the fishing grounds nearby (Van Eerden *et al.* 1991). Whenever these deteriorate, the birds have to move further afield, which implies an increase in their energy expenditure (Platteeuw & Van Eerden 1995) and a decrease in number of young fledged (Van Eerden *et al.* 1991). Fishing efforts, as expressed by daily amount of time spent fishing, are at their maximum during the period of chick rearing (Platteeuw & Van Eerden 1995), implying that this period will be decisive in determining each pair's reproductive output.

This paper is aimed at providing a framework for identifying the margins within which the food provisioning of nestling Cormorants by their parents is limiting the reproductive output of a single breeding season. Measurements of body mass increment with age in individual chicks from broods of different sizes are described in relation to both age ranking of each chick within a brood and brood size. Energy needs of the chicks are estimated by equations found by Weathers (1992), relating both total metabolisable energy (*TME*) throughout the nestling period and peak levels of daily metabolisable energy (*PME*) to body mass and age at fledging. Data on parental fishing effort in terms of fishing time in relation to travelling distance (Platteeuw & Van Eerden 1995) and foraging uptake levels are combined to quantify the potential level of food provisioning by parent birds. By comparison of the estimated food requirements per nest with the parents' potentials for food provisioning, it is possible to visualise possible bottlenecks for reproductive output and indicate where further research is needed.

## METHODS

The growth of Cormorant chicks was studied in the Oostvaardersplassen colony, The Netherlands (see Van Eerden *et al.* 1991) in 1982, 1991 and 1992. In 1982 two nests (with 2 and 3 nestlings each) were visited at least weekly from the moment just before hatching up until fledging. In 1991-1992 this was done twice a week at 14 nests with brood sizes of 1 (3), 2 (7) and 3 (4 nests) nestlings. Measurements on growth were carried out in the morning, after the first return of a parent bird with food. The chicks were lifted out of the nests, which were all situated in willows *Salix* spp. at heights of less than 2 m above the ground. Each occasion, body mass and other parameters of structural size were measured. These included wing length, culmen length and bill depth (at base). Body mass was determined to the nearest 5 g, using a pesola spring balance. Measurements continued up until the moment that the chicks started to jump out of the nests at our approach (at an age of 23-41 days) and thus became virtually impossible to catch. In some of the nests initial clutch sizes were larger than the brood sizes indicated here, but either some of the eggs did not hatch and/or the youngest chicks died within the first week.

For all chicks growth rate (in $g \cdot d^{-1}$) was determined during the period of linear growth (between 5 and 30 days of age). In order to detect possible effects of age ranking within a brood (oldest chick was ranked 1, second 2 and third 3) and brood size on growth rate, an analysis of variance (ANOVA) was carried out to determine the separate effects of age ranking and brood size (Norusis 1990). Logistic growth curves (according to Ricklefs 1967) can only be fitted accurately, when data are available for the entire growth trajectory from hatching until reaching asymptotic body mass. Therefore, they were fitted only to the data of 14 chicks for which also measure-

ments after the age of 30 days were available. These curves represent the equation:

(1) $M = A/(1 + e^{-k\cdot(t-t(i))})$

where $M$ = body mass (g), $A$ = asymptotic body mass (g), $k$ = growth rate constant ($d^{-1}$), $t$ = age (d) and $t(i)$ = age at point of inflection (d). The growth parameters $A$, $k$ and $t(i)$ were estimated in an iterative non-linear regression model (Norusis 1990).

Estimates of *TME* and *PME* of each of the chicks were derived from equations presented by Weathers (1992) based on interspecific data analyses:

(2) $TME = 6.65 \cdot M^{0.852} + t_{fl}^{0.710}$

(3) $PME = 11.69 \cdot M^{0.9082} + t_{fl}^{-0.428}$

where $M$ is body mass at fledging (g) and $t_{fl}$ is age at fledging (d). For the 14 chicks in which logistic growth curves have been fitted, $M$ was estimated by $A$ and $t_{fl}$ by twice the value for $t(i)$.

During the 1982 breeding season 18 Cormorant nests in the colony of Oostvaardersplassen were frequently monitored for entire daylight periods throughout the season (cf. Platteeuw & Van Eerden 1995). Nest attendance of both parents was scored every 10 minutes. Absences exceeding 30 minutes coincided very well with the general pattern of foraging flights as recorded for the entire colony and were therefore recorded as fishing trips outside the colony. The 18 nests were watched for eight days during the period of 1-22 days after the hatching of the first chick. 'Parental fishing effort' is defined here as the total amount of time spent in fishing trips, expressed per pair. These data have been used to quantify parental effort expressed in time spent fishing and potential food provisioning in relation to number of offspring.

## RESULTS

### Growth measurements

Growth rate between 5 and 30 days of age ranged from 56.36 to 102.77 $g \cdot d^{-1}$ (average 74.86 $g \cdot d^{-1}$, *SD* 11.60, $n$ = 34; Table 1). Growth rate tended to be slightly higher among chicks of larger broods, but decreased among siblings with diminishing age (Table 2). The positive effect of brood size on growth rate was not significant ($F_{2,28}$ = 3.241, $p$ = 0.054, ANOVA), but age ranking showed a significant negative influence ($F_{2,28}$ = 3.835, $p$ = 0.034). Interaction between brood size and age ranking was not significant ($F_{1,28}$ = 0.252, $p$ = 0.620).

Examples of individual growth patterns are shown for some of the 14 chicks that were measured beyond an age of 30 days (Fig. 1). The last recorded body mass among these nestlings provided only a slight underestimate of the best estimate for asymptotic body mass $A$ obtained from the non-linear regression. While the last recorded mass ranged from 1720 to 2500 g (average 1980 g, *SD* 206.1, $n$ = 14), asymptotic body mass $A$ ranged from 1781 to 2440 g (average 2042 g, *SD* 189.4, $n$ = 14). Asymptotic fledging mass was positively correlated with growth rate between 5 and 30 days ($r$ = 0.655, $p$ < 0.01), but only 43% of the variance was explained. The three logistic growth parameters were not significantly influenced by either brood size and/or age ranking of the chick within a brood (ANOVA).

### Energy requirements

Estimated *TME* for the 14 chicks measured beyond 30 days of age ranged from 46 046 to 68 792 kJ (average 57 168 kJ, *SD* 5710.0, $n$ = 14) and *PME* from 2053 to 3022 $kJ \cdot d^{-1}$ (average 2530 $kj \cdot d^{-1}$, *SD* 237.7, $n$ = 14). The fastest growing chick (growth rate 102.77 $g \cdot d^{-1}$) showed estimated *PME* and *TME* values of respectively 40 and 47% more than the slowest growing chick (growth rate 56.36 $g \cdot d^{-1}$). Nonetheless, no noticeable relationship was found between growth rate and estimated *TME* ($r^2$ = 0.027, $n$ = 14). Estimat-

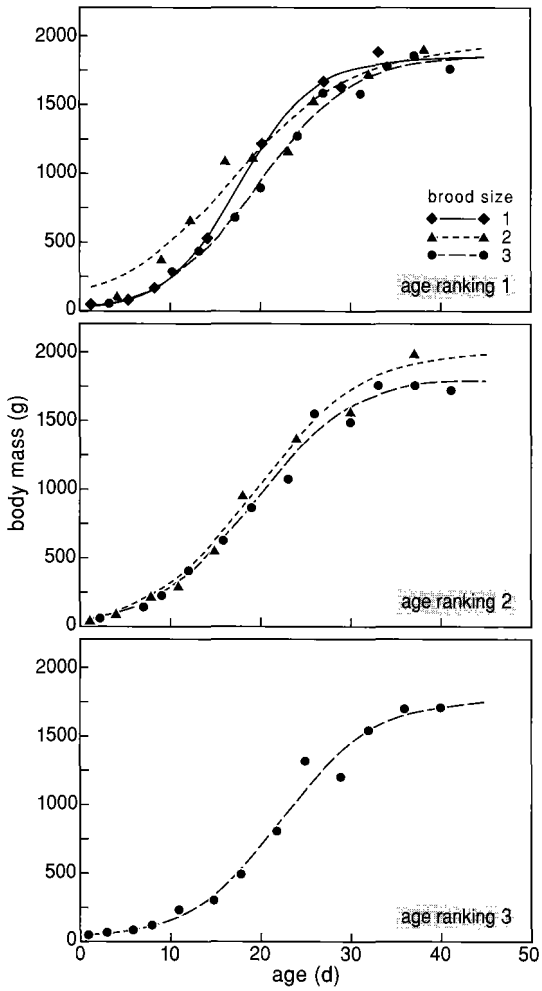


**Fig. 1.** Examples of growth (body mass increment) in six selected Cormorant chicks of different age ranking within their brood (first, second and third-born), that have been measured for over 30 days of age. Growth curves are fitted according to logistic curves (equation $M = A/(1 + e^{-k*(t-t(i))})$; Ricklefs 1967), using non-linear regression for estimating $A$, $t(i)$ and $k$. Growth parameters were not significantly influenced by either age ranking or brood size.

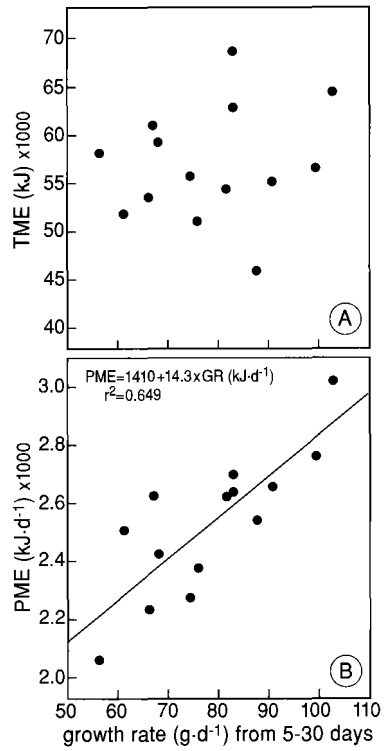


**Fig. 2.** Relationship between growth rate per chick (in $g \cdot d^{-1}$) at period of linear growth (5 to 30 days), (A) estimated total metabolised energy (*TME*; kJ), (B) estimated peak daily metabolised energy (*PME*; $kJ \cdot d^{-1}$). Energy estimates were made according to Weathers (1992).

ed *PME* was, however, positively correlated with growth rate ($r^2 = 0.649$, $n = 14$; Fig. 2).

In spite of the positive relationship between growth rate and *PME* and the negative relationship between age ranking and growth rate, no significant influence of age ranking on *PME* could be detected among the 14 chicks measured longest ($F_{2,8} = 0.106$, $p = 0.901$; ANOVA). Age ranking did not influence the level of estimated *TME* either, nor did brood size influence either *PME* or *TME* (for age ranking on *TME* $F_{2,8} = 0.149$, $p = 0.864$ and for brood size on *PME* and *TME* $F_{2,8} = 0.038$, $p = 0.963$ and $F_{2,8} = 0.057$, $p = 0.945$ respectively). This is undoubtedly caused by the fact that all logistic growth parameters ($A$, $t(i)$ and $k$) turned out to be independent of brood size and age ranking.

## Parental fishing effort and brood size

Among nine nests with three nestlings,

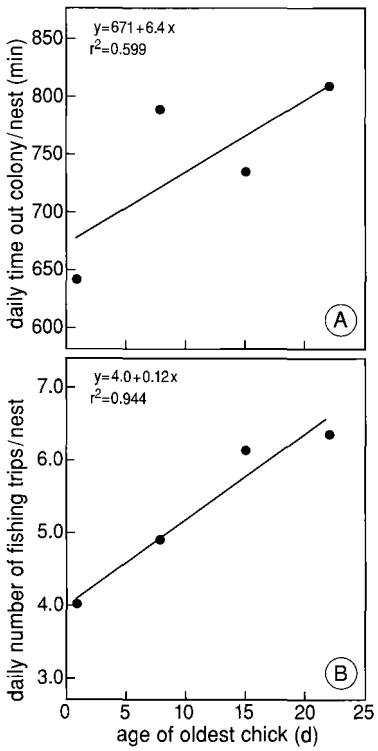


**Fig. 3.** Parental fishing effort in parents with three chicks as a function of age of the first-born chick, (A) mean daily time out of colony per pair, (B) mean number of fishing trips per pair; $n$ = 4 nest-days with similar ages of the first-born on the nests concerned.

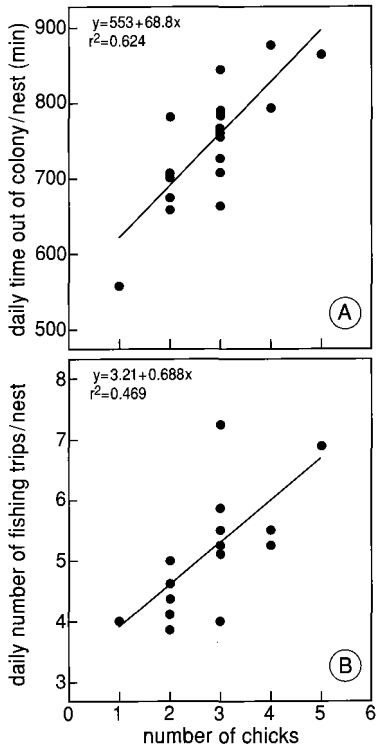


**Fig. 4.** Parental fishing effort as a function of brood size, (A) mean daily time out of colony per pair, (B) mean number of daily fishing trips per pair; $n$ = 18 nest-days during the first 22 days after hatching of the first chick.

followed for four days in which the age of the chicks coincided, both daily time outside the colony and number of fishing trips per pair increased with the age of the first-born chick (Fig. 3). The number of chicks to be fed also determined the daily parental fishing effort as expressed by the daily amount of time a pair spent outside the colony (Fig. 4 A). The parents with a larger brood achieved a higher fishing effort by making more fishing trips per day (Fig. 4 B) rather than by increasing the duration of each trip. This suggests an upper limit to the fish load they are able to carry to the nest. We were, however, unable to determine whether parents with larger broods were able to enhance their foraging uptake.

## DISCUSSION

### Growth rate as a means of energy saving

The suggestion that, apart from brood size, growth rate of nestling birds could be a means of energy saving for their parents (Lack 1968, Ricklefs 1968) was later dismissed by Ricklefs (1969, 1976, 1984) on mainly theoretical considerations. He predicted only a very slight and insignificant contribution of growth rate to nestling energy requirements. Nonetheless, recent analyses of interspecific differences in growth patterns and corresponding energy expenditure have shown that slower growing species have considerably lower energetic costs in both *TME* and *PME* (Weathers 1992). This can, at least

**Table 1.** Growth rates (in g·d-1) of 34 individual Cormorant chicks from different brood sizes and of different age ranking between 5 and 30 days of age, assuming growth to be linear.

| Brood size | Age ranking | Growth rate ($g \cdot d^{-1}$) | $r^2$ |
|---|---|---|---|
| 1 | 1 | 76.06 | 0.974 |
| 1 | 1 | 77.25 | 0.956 |
| 1 | 1 | 56.87 | 0.976 |
| 2 | 1 | 76.22 | 0.978 |
| | 2 | 68.23 | 0.966 |
| 2 | 1 | 61.26 | 0.910 |
| | 2 | 66.60 | 0.968 |
| 2 | 1 | 73.50 | 0.988 |
| | 2 | 72.81 | 0.982 |
| 2 | 1 | 65.61 | 0.960 |
| | 2 | 61.90 | 0.937 |
| 2 | 1 | 57.74 | 0.958 |
| | 2 | 78.12 | 0.976 |
| 2 | 1 | 81.99 | 0.957 |
| | 2 | 71.13 | 0.944 |
| 2 | 1 | 75.00 | 0.949 |
| | 2 | 69.44 | 0.950 |
| 2 | 1 | 99.42 | 0.980 |
| | 2 | 90.67 | 0.982 |
| 3 | 1 | 82.66 | 0.991 |
| | 2 | 87.50 | 0.970 |
| | 3 | 67.28 | 0.965 |
| 3 | 1 | 96.07 | 0.993 |
| | 2 | 86.09 | 0.988 |
| | 3 | 67.76 | 0.984 |
| 3 | 1 | 102.77 | 0.995 |
| | 2 | 81.72 | 1.000 |
| | 3 | 82.82 | 0.992 |
| 3 | 1 | 74.12 | 0.955 |
| | 2 | 78.97 | 0.964 |
| | 3 | 60.70 | 0.983 |
| 3 | 1 | 74.38 | 0.980 |
| | 2 | 66.10 | 0.966 |
| | 3 | 56.36 | 0.909 |

partly, be attributed to relatively low levels of basal metabolic rate (*BMR*) in chicks of slow-growing species (Drent & Klaassen 1989, Klaassen & Drent 1991, Klaassen *et al.* 1992). Intraspecific differences in energetic costs of tern chicks of varying growth rates, although not attributable to relatively lower levels of *BMR* (Klaassen & Bech 1992), are in the same order of magnitude as the interspecific differences (Klaassen *et al.* 1992). For estimating intraspecific variation of *TME* and *PME* in Cormorant chicks, the use of the interspecific equations found by Weathers (1992) is therefore justified.

Calculated *PME* was indeed found to increase with growth rate, the fastest growing chicks requiring over 45% more energy per day than the slowest growers. The estimated energy savings of slow growth were similar to those found empirically in laboratory experiments for Common *Sterna hirundo* and Sandwich Tern *S. sandvicensis* chicks (Klaassen *et al.* 1992), but rather higher than suggested by field work for Sooty Tern *S. fuscata* (Ricklefs & White 1981).

Among the 34 chicks measured, age ranking alone proved to have a significant negative influence on growth rate. Younger chicks within the same brood will therefore have lower *PME* values than their older siblings. Nonetheless, the combined influence of age ranking and brood size was practically nil. Therefore, average energetic requirements per nest could be reliably estimated by multiplying a chick's individual needs with brood size. Values of *PME* obtained this way deviated by a range of -3 to +1% from those calculated from age and brood size specific growth rates (Table 2) and the relationship between growth rate and *PME* (Fig. 2 B). A lowered growth rate may serve to lessen parental energy investment at the period of maximum needs. Within the range of 1-3 chicks per brood, however, the decrease in growth rate in younger siblings is too small to have any noticeable influence on the amount of parental investment. Chicks are likely to maintain their growth rate as high as physiologically possible within the constraints of their parents food provisioning abilities (always make the best of a bad job). This way, they would enhance their chances of post-fledging survival. Lowered growth rates in younger siblings (and larger broods) will generally origi-

**Table 2.** Average values for linear growth rate (in $g \cdot d^{-1}$) within different classes of brood size age ranking and a combination of these two factors.

| | Brood size | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | Overall |
| Age ranking | | | | |
| 1 | 70.06 | 73.84 | 86.00 | 76.93 |
| 2 | - | 72.36 | 80.08 | 75.33 |
| 3 | - | - | 66.98 | 66.98 |
| Overall | 70.06 | 73.10 | 77.69 | 74.86 |

nate from adapting the needs to the working capacity of the parents rather than from meeting the parents half-way.

## Food requirements of growing chicks

In order to get a rough idea of the amount of food a parent Cormorant would have to take to the nest, the estimate of the average chick's *TME* and *PME* ($n$ = 14; only for the chicks measured longest) were converted to fresh fish mass (*FM*). Assuming an assimilation efficiency of 0.8, which is a rather universal value for fish-eating birds (Castro *et al.* 1988), and a caloric value of 5.0 $kJ \cdot g^{-1}$ *FM* (Buijse & Houthuijzen 1993), the food intake of a chick was estimated at an average of about 386 g *FM* per day throughout the nestling period and at a maximum of 632 $g \cdot d^{-1}$. These values represent slightly higher food needs of Cormorant chicks than suggested by the findings of Van Dobben (1952) who hand-raised 3-weeks old Cormorant chicks till fledging mass on different daily rations. He found 200 g of fish per day to be insufficient for normal growth, while birds receiving 300 g were still less well-fed than control samples.

A considerable source of error was introduced by the process of estimating asymptotic body mass $A$ and fledging age $t_{fl}$ (twice the value for $t(i)$). Considering upper and lower 95%-confidence limits for these two logistic growth parameters, mean daily ration of the chicks may range from 356 to 413 $g \cdot d^{-1}$ *FM* and maximum daily ration from 528 to 753 $g \cdot d^{-1}$. These ranges should be kept in mind when considering the parental responses to the chicks' needs.

## Limits to parental fishing effort

It has been shown that parents which have to feed more young spend more time outside the colony because of an increase in daily fishing trips (cf. Fig. 4). Actual fishing time can be estimated for each trip by subtracting flying time from the colony to the fishing site and back from total time out. Since the duration of a fishing trip depends primarily on the flying time (Platteeuw & Van Eerden 1995), the increase in actual fishing time per day achieved by making more trips becomes less at longer travelling distances. Thus in Cormorants the flight distance to and from the foraging grounds imposes an energetic plateau to the parents' working level.

For varying travelling distances the necessary rates of food provisioning by Cormorant parents to raise a brood of a certain size can be assessed in relation to their broods' average and maximum requirements (Fig. 5). For this purpose, the time a pair actually spent fishing per day was multiplied by different foraging uptake levels, positioned around the empirically found average of about 3 $g \cdot min^{-1}$ *FM* for incubating adults in April (Voslamber 1988, Platteeuw & Van Eerden 1995). This provided an estimate of the total amount of fish to be caught each day to satisfy the needs of their chicks and themselves. Despite an increase in daily energy expenditure of the adults with flying distance, the actual daily fish consumption of an adult remained very much the same: about 330 $g \cdot d^{-1}$ *FM* per parent (Platteeuw & Van Eerden 1995). After subtraction of the parents' own food requirements, potential food provisioning rates for each of three flying distances were expressed as linear functions of brood size in Fig. 5. Five uptake levels, ranging from 2.5 $g \cdot min^{-1}$ to 5.0 $g \cdot min^{-1}$ *FM*, were distinguished. Whenever these functions give higher values than the line indicating the chicks' needs, food provisioning is likely to be sufficient to raise the corresponding brood

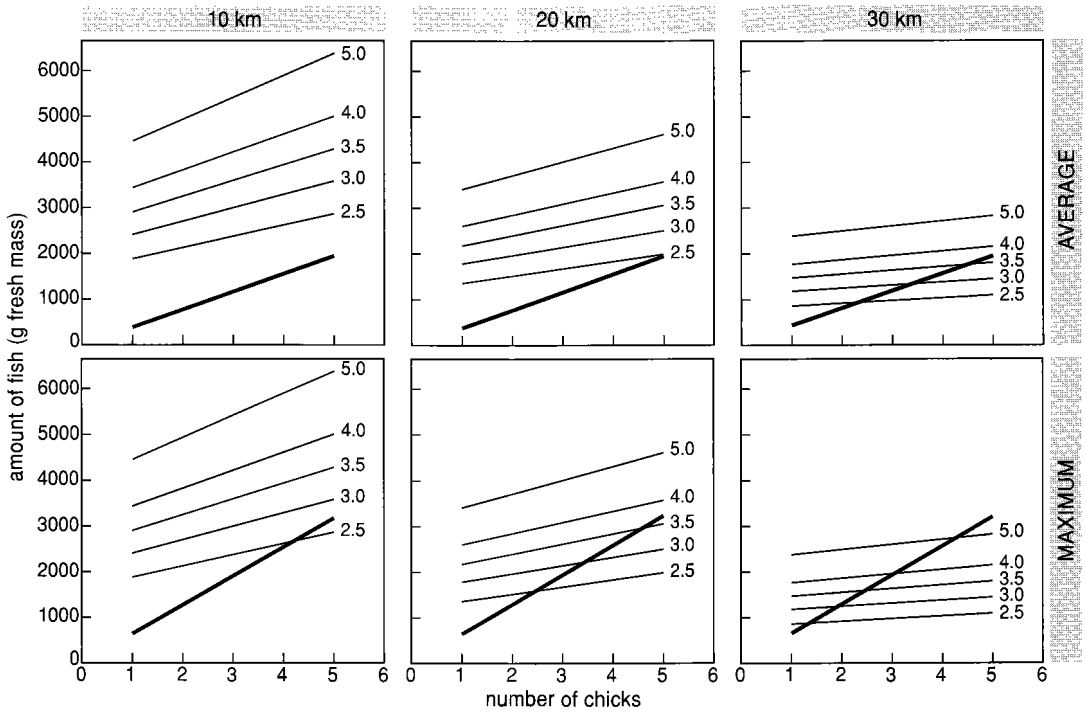


**Fig. 5.** Relationship between calculated mean and maximum daily food needs per nest and brood size (fat lines), compared with the relationship between observed food provisioning per nest per pair (after subtraction of the parents' own fixed needs; Platteeuw & Van Eerden 1995) and brood size. Assumed fishing uptake levels of 2.5, 3.0, 3.5, 4.0 and 5.0 g·min$^{-1}$ *FM* (thin lines) and travelling distances between colony and fishing site of 10, 20 and 30 km are indicated. In each figure the shaded area indicates combinations of fishing success and brood size that will not lead to a successful raising of the complete brood. Uptake levels around 3.0 g·min$^{-1}$ *FM* were observed in the field (1982).

size. Comparison of the average and maximum daily food needs per brood of a certain size to the supposed yields of parental fishing effort at varying flying distances and foraging uptake levels shows that the period of maximum food requirements of the chicks represents the greatest bottleneck in raising young (Fig. 5). Only at a foraging distance of 10 km and uptake levels of 3.0 g·min$^{-1}$ *FM* or more, feeding enough food to raise five young is possible, but already at a distance of 20 km an uptake level of at least 5.0 g·min$^{-1}$ *FM* is required to help a brood of five through their period of maximum energy requirements.

These calculations suggest that, although the total amount of food to be provided to the young undoubtedly poses its constraints on the parents, a factor even more directly limiting brood size and number of chicks actually fledging might be the maximum daily amount of food to be brought to the young in the course of their development. This would agree well with earlier suggestions (Ricklefs 1976, Klaassen *et al.* 1992). When the data on parental fishing effort were collected, in 1982, the colony size was much less than it was in the 1990s (Van Eerden & Gregersen 1995). Moreover weather conditions, and thus fishing opportunities were better (*cf.* Van Eerden & Voslamber 1995). It is, therefore likely that in the 1990s both the higher breeding density and the rather unfavourable weather conditions have enhanced the energetic contraints on the parents'

working level, hence causing even lower reproductive outputs then indicated here.

Parental 'quality' in Cormorants seems to express itself in the first place by the number of daily fishing trips they make. Moreover, the calculations carried out above indicate that an ability to enhance fishing uptake level would also greatly contribute to parental quality. Thus, a higher working level may lead to a higher number of offspring within a single breeding season. On the other hand, the positive correlation found between working level and number of fledging chicks can also be explained the other way round: the parents increase their efforts to meet the higher energetic needs. Since we have seen that travelling distance as well as uptake level can affect parental food provisioning considerably, individual differences in foraging behaviour (choice of fishing site, fishing efficiency) among pairs of parents may also determine reproductive output. Most of the Cormorants that always follow the main social fishing group (Van Eerden & Voslamber 1995) are suspected to suffer considerable mass losses throughout the breeding season because of a high level of energy expenditure and a relatively low foraging uptake (Platteeuw & Van Eerden 1995). However, individual pairs of which at least one partner follows a foraging strategy that keeps it closer to the colony and/or permits it to fish more successfully (cf. Voslamber *et al.* 1995) can easily catch enough fish to maintain their body reserves and at the same time provide enough food to their offspring to raise up to five hatchlings to fledging mass. Also, socially fishing birds which can consistently maintain a favourable position within the flock may be able to do better than 'average' with respect to foraging uptake (Van Eerden & Voslamber 1995). Future work will concentrate on establishing individual differences in adult foraging strategies (including fishing yield). These data, in combination with direct measurements on gross energy intake and/or daily metabolised energy of individual growing chicks as well as with more prolonged series of growth measurements, should further narrow down the margins for good reproductive output of individual pairs as outlined here.

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## SAMENVATTING

De groei van 34 jonge Aalscholvers uit broedsels van verschillende groottes wordt beschreven aan de hand van de toename in het lichaamsgewicht. Groeisnelheden zijn berekend over het traject van (nagenoeg) lineaire groei tussen dag 5 en dag 30. De groeisnelheid bleek licht af te nemen bij later geboren kuikens uit een zelfde nest, maar in combinatie met broedselgrootte bleek er geen significante beïnvloeding van groeisnelheid op te treden. De groeiparameters: asymptotisch uitvlieggewicht, groeisnelheidscoëfficiënt en leeftijd op het moment van inflectie, zijn geschat voor de 14 kuikens die tot na dag 30 zijn gevolgd en al een afvlakking van het gewicht te zien gaven.

Met behulp van rekenkundige verbanden tussen totale en maximale metaboliseerbare energiebehoefte enerzijds en uitvlieggewicht en uitvliegleeftijd anderzijds (opgesteld via een interspecifieke beschouwing, Weathers 1992), zijn schattingen gemaakt van de energiebehoeften van de jongen. Het gebruik van deze formules voor intraspecifieke verschillen wordt gerechtvaardigd. De snelste groeiers vertoonden een maximale energiebehoefte van 3022 kJ per dag, de traagste van 2050 kJ per dag. De totale energiebehoefte over de periode in het nest varieerde van 46 000 tot 69 000 kJ, gemiddeld 1300-1800 kJ per dag. Gemiddeld werd de energiebehoefte van de snelste groeier 40% hoger geschat dan die van de traagste en gedurende de periode van maximale behoefte zelfs 47% hoger. Grotere broedsels hebben een hogere energiebehoefte, te schatten door vermenigvuldiging van de gemiddelde individuele behoefte van een kuiken te vermenigvuldigen met de broedselgrootte. Deze benadering wordt gerechtvaardigd door het feit dat groeisnelheid niet beïnvloed werd door de combinatie van broedselgrootte en leeftijdsverschillen binnen één broedsel.

De ouders van grotere broedsels bleken dan ook meer tijd aan vistochten te besteden door vaker de kolonie te verlaten. De 'bottleneck' voor het grootbrengen van jongen doet zich voor tijdens de periode van maximale energiebehoefte, als elk jong 632 g vis per dag nodig heeft. Bij een vliegafstand kolonie-visplaats van 30 km kan dan slechts door minimaal 4 $g \cdot min^{-1}$ vis te vangen nog juist voor drie jongen voldoende voedsel worden meegenomen. De meeste oudervogels lijken hun energieinvestering te verhogen als ze grotere broedsels hebben te verzorgen. Ook wordt duidelijk gemaakt dat het volgen van een andere

dan modale fourageerstrategie (dichterbij blijven en/of meer vis vangen per tijdseenheid) tot verhoogd reproductief succes kan leiden. Meer gedetailleerd onderzoek naar individuele verschillen zal moeten uitwijzen welke mechanismen er bestaan.